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Kokko, Hanna

**Abstract:** Biological diversity abounds in potential study topics. Studies of model systems have their advantages, but reliance on a few well-understood cases may create false impressions of what biological phenomena are the norm. Here I focus on facultative sex, which is often hailed as offering the best of both worlds, in that rare sex offers benefits almost equal to obligate sex and avoids paying most of the demographic costs. How well do we understand when and why this form of sexual reproduction is expected to prevail? I show several gaps in the theoretical literature and, by contrasting asynchronous with synchronous sex, highlight the need to link sex theories to the theoretical underpinnings of bet hedging, on the one hand, and to mate limitation considerations, on the other. Condition-dependent sex and links between sex with dispersal or dormancy appear understudied. While simplifications are justifiable as a simple assumption structure enhances analytical tractability, much remains to be done to incorporate key features of real sex to the main theoretical edifice.

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## SYMPOSIUM

# When Synchrony Makes the Best of Both Worlds Even Better: How Well Do We Really Understand Facultative Sex?\*

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**ABSTRACT:** Biological diversity abounds in potential study topics. Studies of model systems have their advantages, but reliance on a few well-understood cases may create false impressions of what biological phenomena are the norm. Here I focus on facultative sex, which is often hailed as offering the best of both worlds, in that rare sex offers benefits almost equal to obligate sex and avoids paying most of the demographic costs. How well do we understand when and why this form of sexual reproduction is expected to prevail? I show several gaps in the theoretical literature and, by contrasting asynchronous with synchronous sex, highlight the need to link sex theories to the theoretical underpinnings of bet hedging, on the one hand, and to mate limitation considerations, on the other. Condition-dependent sex and links between sex with dispersal or dormancy appear understudied. While simplifications are justifiable as a simple assumption structure enhances analytical tractability, much remains to be done to incorporate key features of real sex to the main theoretical edifice.

**Keywords:** facultative sex, cost of sex, synchrony, mate searching, mathematical modeling, bet hedging.

## Introduction

I recently had the fortune of lunching with Georgina Mace and other panel members of a grant funding body. In the conversation, Mace reminded us of how lucky we are, working in a field where most researchers are generous and open about their ideas. She reflected on whether the general niceness of a field might be a function of the ratio of the number of things (objects, topics) available to study and the number

of people wanting to study them. The abundance of organisms with diverse life histories, genetic architectures, ecological settings, and idiosyncratic quirks of natural history means that researchers need not be particularly anxious about losing their territory to others with similar ideas—and most of us, fortunately, understand this.

This brings about a nice atmosphere (one that may well differ from that of other fields of scientific enquiry) but also creates a challenge. The immense diversity of features of biological systems means we all must find a balance between admiring the idiosyncratic and seeking generalities in life's messages. One approach is to rely disproportionately on model organisms and tacitly assume that they reflect life as a whole. This approach has its advantages: having in-depth knowledge of *Escherichia coli*, *Caenorhabditis elegans*, *Saccharomyces cerevisiae*, maize, *Arabidopsis thaliana*, *Ciona intestinalis*, *Chlamydomonas reinhardtii*, *Drosophila*, zebra fish, and *Mus* and *Peromyscus* mice—the list discussed in eLife's recent collection of feature articles on the natural history of model organisms (Alfred and Baldwin 2015)—undoubtedly leads to better science than a superficial look at 100,000 species. A highly selective approach to what we study in the tree of life comes, however, with a significant danger of bias: not all arthropod life obeys *Drosophila* rules, for example, with respect to sexual selection (Zuk et al. 2014). A partial answer may be found in widening the scope of genomic work to encompass more species (Alfred and Baldwin 2015; Russell et al. 2017). This answer is, however, bound to retain a one-sided nature if not accompanied by equivalently broad efforts to understand the ecology and natural history of each case (Futuyma 1998; Kokko et al. 2017).

There is no top-down control of scientific effort spent across taxa. While I believe that the benefits of a bottom-up approach far outweigh its costs (and the scientific community thus has a duty to defend the freedom of each researcher to choose what to study), this is not to say there is no downside. Individual choices collectively lead

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to taxonomic chauvinism, the tendency to study species that in some sense are close to humans (Kokko 2017; Troudet et al. 2017). Parallel to this, there are very good reasons to study phenomena (or species) that are common and to simplify their features in theoretical work to the bare minimum, to help focus on the (probable) key causalities. This is probably a faster route to general messages than focusing on the idiosyncratic and the odd, but a focus on the familiar and on the common does not take full advantage of the general messages that can be found when thinking about rare evolutionary outcomes—or even absent ones. Darwin's thinking during his voyage on the *Beagle* was focused not only on what he saw but also on what he did not see: oceanic islands rarely had frogs, even if there was habitat on offer that appeared suitable (Darwin 1859). Such biogeographic patterns are unexpected if species have been created on site to match their environment, while a vision of species descending from ancestral forms, with travel difficulties that depend on the species' traits, explains this with ease. True evolutionary insight can be gained from a lack of examples belonging to a certain category, and Darwin made ample use of this type of insight.

The reasons behind rarity and absence are not always as easy to explain as in the case of oceanic island fauna. The particular case I will focus on here is that of sexual reproduction in its facultative mode. It comes with a special twist: its perceived rarity might be just that—a perception. Textbooks explaining why sex is problematic often explain the conundrum with the cost of males paid by an obligate sexual anisogamous lineage, but once the full diversity of reproductive modes is taken into account, facultative sex proves common (particularly so, but not only if, vegetative modes are also included as asexuality). Facultative sex not only offers ample opportunity to reflect on whether perceived rarity also corresponds to real rarity, it also allows me to reflect on modeling choices that are made for convenience versus their abundance in reality. I will discuss this contrast in the specific setting of whether facultative sex occurs in synchrony (such that many or even most individuals in a subpopulation engage in sex in a particular generation, while other generations have much less sex) or asynchronously.

Facultative sex is often described as offering most of the advantages of sex (rare sex speeds up adaptation and/or avoids genome decay almost as well as obligate sex; Green and Noakes 1995; Park and Krug 2013; Hojsgaard and Hörandl 2015; Burke and Bonduriansky 2017) while paying very little of the costs (since most generations are asexual and thus demographically efficient). The demographic cost may even itself help speed up adaptation if relatively maladapted individuals are more likely to pay the cost, which can happen under condition-dependent sex (Hadany and Otto 2009). Facultative sex can occur in contexts

where separate males and females exist (the term “cyclical parthenogenesis” is often employed in these contexts, e.g., *Daphnia* [Decaestecker et al. 2009], aphids [Simon et al. 2002], or various rotifers [Stelzer 2011]), in hermaphrodites (e.g., flatworms [Ramm 2017], numerous plants [Mogie 2011]), or—very commonly—in situations involving mating types rather than anisogamous sexes (the typical situation across a broad range of microbial and fungal sex, including model organisms such as *Chlamydomonas* and yeast; Sager and Granick 1954; Ropars et al. 2012; Speijer et al. 2015; Weedall and Hall 2015; Nieuwenhuis et al. 2018).

### Facultative Sex: Why Don't We All Do It?

If facultative sex, at first sight at least, offers the best of both worlds, then evolutionary biologists have to explain why it is not self-evidently the only way that sex occurs. Burt (2000) predicts facultative sex to be susceptible to the invasion of modifiers with ever less frequent sex, unless ecological differences between sexual and asexual progeny provide the necessary stability. Although he does not put the argument in the context of social evolution, one could do so via the tragedy of the commons (Hardin 1968; Rankin et al. 2007). The lineage benefits of sex are not easy to assign to any one individual (Burt 2000). The cost of sex behaves differently: it is an immediate cost paid by a specific individual.

Thus, a cheater could be identified as an individual who performs less of the costly sex and simply taps occasionally into the public good of a well-adapted gene pool. Empirically (or in models), such scenarios could be identified as individuals tending to be less fit if their ancestry has more asexual generations (compared with conspecifics) since the last sex event. Models such as that of Roze (2014), where positive rates of sex are maintained despite low sex being exposed to mutations that give rise to asexuals, fit this analogy to some extent: the lineage benefit builds up over time, and genes facilitating sex remain for multiple generations with the gene combinations produced by sex. If one interprets a modifier for a smaller sex rate as a cheater (note that Roze 2014 did not adopt this language), its success depends on how well it keeps its statistical association with beneficial alleles when reproducing asexually much of the time, with each asexual generation having multiple effects: weakening this association (interpretable as diminished access to the public good), failing to participate in the beneficial buildup (no contribution to public good), and—if sex is costly—the cheater gaining a demographic advantage (the reason why cheating may pay off in social models). These factors are likely to combine nonlinearly, and in Roze (2014), they balance in a way where low-rate modifiers can spread in populations with currently high sex rates, but low sex rates are resistant to modifiers with even lower rates.

Current theoretical work on the evolution of recombination and sex often focuses on the fate of modifiers of recombination in the presence of epistatic fitness interactions (Barton 1995), including cycling epistasis of abiotic or biotic origin (Barton 1995; Gandon and Otto 2007), with subsequent inquiry analyzing the spread of recombination modifiers in stochastic models, where recombination reduces selective interference among loci (e.g., bringing together beneficial alleles in an adapting population; Otto and Barton 1997; Roze and Barton 2006) or in a population subject to recurrent deleterious mutations (Keightley and Otto 2006; Roze and Michod 2010). In haploid populations, recombination modifiers are thought to capture the benefits of breaking apart linkage disequilibria and behave similarly to modifiers of sex, although there are important differences in finite populations (Roze 2014), and the direct costs exhibited by modifiers of recombination differ qualitatively from modifiers of sex. Explicit models of sex have examined the fate of modifiers that alter the frequency of sexual versus asexual reproduction, particularly in the face of within-locus fitness interactions (dominance) that build associations between alleles in a diploid population (e.g., Otto 2003; Roze and Michod 2010; Roze 2014). For a concise and clear summary of model lessons to date, see Hartfield (2016).

Although it is difficult to find a statement in print that the “Why sex?” question is therefore, by and large, resolved, it is possible to hear this at conferences. However, whenever a model focuses on a modifier of recombination, it is geared toward understanding the advantages (or disadvantages) of breaking up established associations between two loci on the same chromosome. Modifiers in this setting do not induce sexual reproduction: outcrossing is assumed to occur in any case, and since the focus of a model is to estimate whether modifiers hitchhike to higher or lower frequencies as a result of becoming linked with alleles under selection, the typical approach is to focus on cases with no direct selection on the modifier itself. While this is good for clarity of any analysis of indirect selection and is, in some models, accompanied by additional results with a direct cost incorporated (e.g., Gandon and Otto 2007), the intentional focus on the no-cost case may have an impact on the perceived ease with which sex, consequently, evolves.

More recent work has taken to heart a point already made by Uyenoyama and Bengtsson (1989): sex comprises a syndrome of diverse processes. In models that explicitly differentiate between sex and recombination, modifiers of an actual rate of sex can cause demographic costs and nevertheless maintain a positive sex rate (though, again, the main analyses sometimes maintain a focus on the cost-free case; e.g., Roze and Michod 2010). Modifiers that impact the rate of sex can escape low-fitness genetic backgrounds (Roze 2014; this is often termed the “abandon-ship” effect;

e.g., Hadany and Otto 2007; Mostowy and Engelstädter 2012), or they can break apart association within genes built by dominance (Otto 2003; Roze and Michod 2010) or between genes built by epistasis (e.g., Roze and Michod 2010). Such benefits may, however, not always be sufficient to overcome the costs of engaging in sex, even if sex rates are low (e.g., fig. 2 in Keightley and Otto 2006). The extent to which the invasion of ever-lower sex rates, as envisaged by Burt (2000), occurs is not entirely easy to assess based on the available literature: some authors contrast a modifier that imposes a specific rate of sex with a modifier that keeps the population asexual (Keightley and Otto 2006), which is a different question from asexuals or very low sex rates being able to invade an initially (facultatively) sexual population; others (Roze and Michod 2010; Roze 2014) employ a mutational structure where low, but not high, sex rates can turn (via mutation) to asexuality. Since the results show that positive rates of sex can nevertheless be maintained (Roze 2014), one could consider the story to be complete, in the sense of countering Burt’s idea: low rates of sex can be stable even in the absence of ecological differences.

But how complete is our understanding of the question? Here I will not attempt to resolve the question for good; I will aim to show that much remains to be done. While there is no reason to complain about models making assumptions for reasons of analytical tractability (and spending more time on results that assume zero costs), there is much reason to see this as an opportunity to relax assumptions in further work. Real-life sex presents us with many patterns that are justifiably ignored in any first—or even tenth or twentieth—model on a topic, but this should only increase one’s appetite for investigating the relevant effects in future models.

The example I will focus on is synchrony. Sex is often triggered by environmental cues, which may be nutrition limitation (e.g., *Chlamydomonas*; Sager and Granick 1954), various abiotic or biotic cues of seasonality (e.g., *Daphnia*; Roulin et al. 2015; Gerber et al. 2018), or an individual’s perception of its own condition (Ram and Hadany 2016). In models, however, synchronous sex is typically absent: matings are assumed to occur in any case (many models of recombination, as discussed above); individuals reproduce sexually with a specific probability (impacted by a modifier allele) but not in synchrony with each other (Keightley and Otto 2006; Hadany and Otto 2007); or individuals split their reproductive effort, in every generation, into an asexually produced and a sexually produced fraction (e.g., Roze 2014).

### Model Details

There are many mechanisms available to introduce a potential benefit of sex into a model (Hartfield and Keightley



2012; Roze 2014; Hartfield 2016). I base my individual-based simulation on the model of Kim and Orr (2005), who considered the faster rate of evolution in a sexual versus asexual population when a modest number of sites can mutate to a beneficial version. In a finite population with a sufficient mutation rate, lineages with different beneficial mutations compete in asexuals (clonal interference causing evolution to be slow via the Hill-Robertson effect) and can therefore fix faster in sexuals as each mutation does not have to arise in a genome that already contains the other (Fisher-Muller effect; Fisher 1930; Muller 1932). There is recent empirical support for clonal interference playing a key role in the evolution of sex (Colegrave 2002; McDonald et al. 2016).

### Genotypes

I model a population of  $N$  diploid hermaphrodites that can be facultative sexuals or asexuals. Obligate sex is not excluded in my setup as the rate of sex can evolve to 1, though such high rates in practice do not evolve in the settings I investigate below. The reproductive mode of each individual is determined by one diploid locus that determines the rate of sex. If both alleles have a positive value, then their mean determines the probability that the individual reproduces sexually. Asexuality is dominant, such that one allelic value of zero is sufficient to make the individual asexual. Note that this is a relatively good approximation of what happens in real transitions to asexuality in systems such as *Daphnia* (Eads et al. 2012) or *Pennisetum* grasses (Conner et al. 2015), though I do not model complications such as the three-locus system involving transposons, identified by Eads et al. (2012). I also leave aside transitions to asexuality via hybridization and polyploidy (Neiman et al. 2014), as my aim is simply to see how rare sex withstands frequent mutations to asexuality, regardless of the way it arose.

My focus is on the contrast between two different scenarios. In the asynchronous scenario, each individual has an independent probability of choosing the sexual reproductive mode (if only one single individual does so in its generation, it can self automatically). In the synchronous scenario, one uniformly distributed random number is drawn in each generation, corresponding to an environmental trigger that is perceived by all members of the facultative sexual population. All individuals whose sex rates (mean of two alleles) are above this trigger value perform a sexual cycle. A strong enough trigger—that is, low enough value of the random number—means that all facultative sexuals have sex, while a somewhat less strong trigger means that only those with a higher rate of sex do.

The sex rate locus can experience two types of mutation. An asexuality mutation occurs at a rate  $\mu_A$  per locus (no back mutation) and changes the allelic value to 0, while a

rate mutation, occurring at a rate  $\mu_R$  per locus, makes an allelic value  $x$  mutate to  $e^{(\ln x) + \epsilon}$ , where  $\epsilon \sim N(0, 1)$ . New allelic values exceeding 1 are capped to 1. This construction is used to make the probability of halving (or doubling) the rate equally likely whether the rate so far was high or low (up to a point, as higher than 100% rates cannot logically occur) and to exclude the possibility that a rate mutation per se leads to asexuality: even if  $\epsilon$  is a large negative number, the function  $e^{\ln x + \epsilon}$  remains positive (but can be very small, e.g., sex every  $10^6$  generations).

The  $n$  other diploid loci determine fitness components other than the cost of sex, and they are all initialized with a wild-type allele 0. They mutate (rate  $\mu_B$ ) to a beneficial allele, with no back mutation. Each beneficial allele is dominant and brings about a multiplicative fitness benefit of magnitude  $s$  (i.e., no epistasis). Thus, with  $n = 10$  loci (the value of  $n$  used in the examples of all the figures), the maximum fitness achievable by any individual is  $(1 + s)^{10}$ . Simulation runs are continued until either asexuality (proportion of individuals with at least one sex rate allele with the value 0) reaches a threshold frequency (50% or fixation, depending on the question) or when the population produces its first individual with fitness  $(1 + s)^{10}$ , as the adaptation process will no longer follow equivalent rules afterward (a subset of the population is already at a fitness peak). All loci recombine freely.

I also ran two types of control simulations: in the first set, the sex locus determines the mode of reproduction as above, but none of the other loci are expressed (while they still mutate as above). This helps contrast the main findings against expectations when sex is costly but brings about no benefit. The different effects of synchronous and asynchronous sex on effective population size are maintained in this no-benefit set of simulations: in particular, asynchronous sex may lead to selfing if sex is rarely expressed, and this can significantly reduce  $N_e$  (Kamran-Disfani and Agrawal 2014). In another control set of simulations termed “sex neutral,” sex alleles are never expressed, and all reproduction is asexual while keeping the beneficial alleles expressed; this is done to find a baseline expectation for the persistence of sex against recurrent mutations to asexuality.

### Life Cycle

The population size is kept constant at  $N$ , and generations are discrete. The mothers of each offspring are chosen first, and the sire is assigned next. Each individual's propensity to be chosen as the mother is

$$p_i = \begin{cases} (1 + s)^{k_i} & \text{if currently asexual,} \\ (1 - c)(1 + s)^{k_i} & \text{if currently sexual.} \end{cases}$$

Here  $c$  is the cost of sex ( $0 \leq c \leq 1$ , though in practice an upper limit of 0.5 is relevant if one wishes to model costs

up to twofoldness, i.e., the halving of demographic output),  $k_i$  is the number of loci at which individual  $i$  has at least one beneficial allele, and “currently asexual” or “currently sexual” reflects the phenotypic choice made by the individual in the current generation regarding its reproductive mode. Note that the model ignores any permanent costs of facultative sexuality that would have to be paid in asexual generations (i.e., costs of phenotypic plasticity; Auld et al. 2010).

The sires are thereafter chosen for those offspring whose mothers are currently sexual. All sexual individuals are potential sires, with propensities

$$q_i = (1 + s)^{k_i}.$$

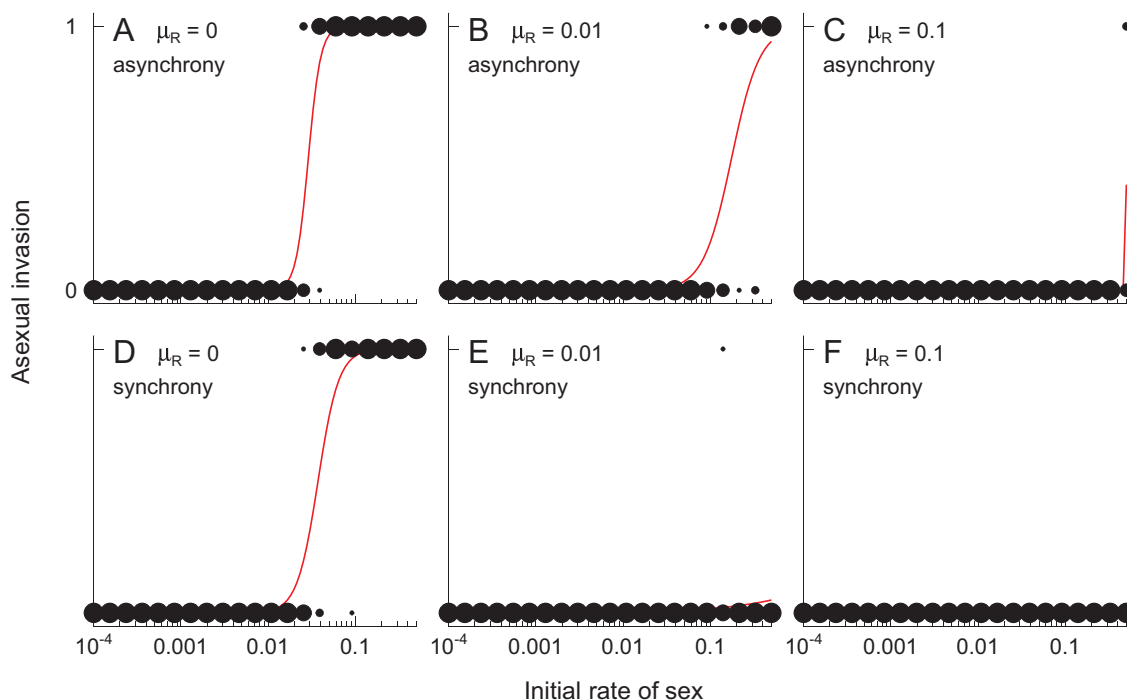
Note that the cost of sex is irrelevant for this expression, as all potential sires are sexual and compete with each other. The sire is chosen independently for each offspring of a given mother.

Propensities translate to actual parentage in a probabilistic manner; for example, if a population only had three potential sires, one with propensity 1.0, another with 1.01, and a third with 1.0201 (the outcomes for 0, 1, or 2 ben-

eficial alleles if  $s = 0.01$ ), then the first individual is chosen with probability  $1/3.0301$ , the second with probability  $1.01/3.0301$ , and the third with probability  $1.0201/3.0301$ . Mutations then occur, and the parental generation dies.

## Results

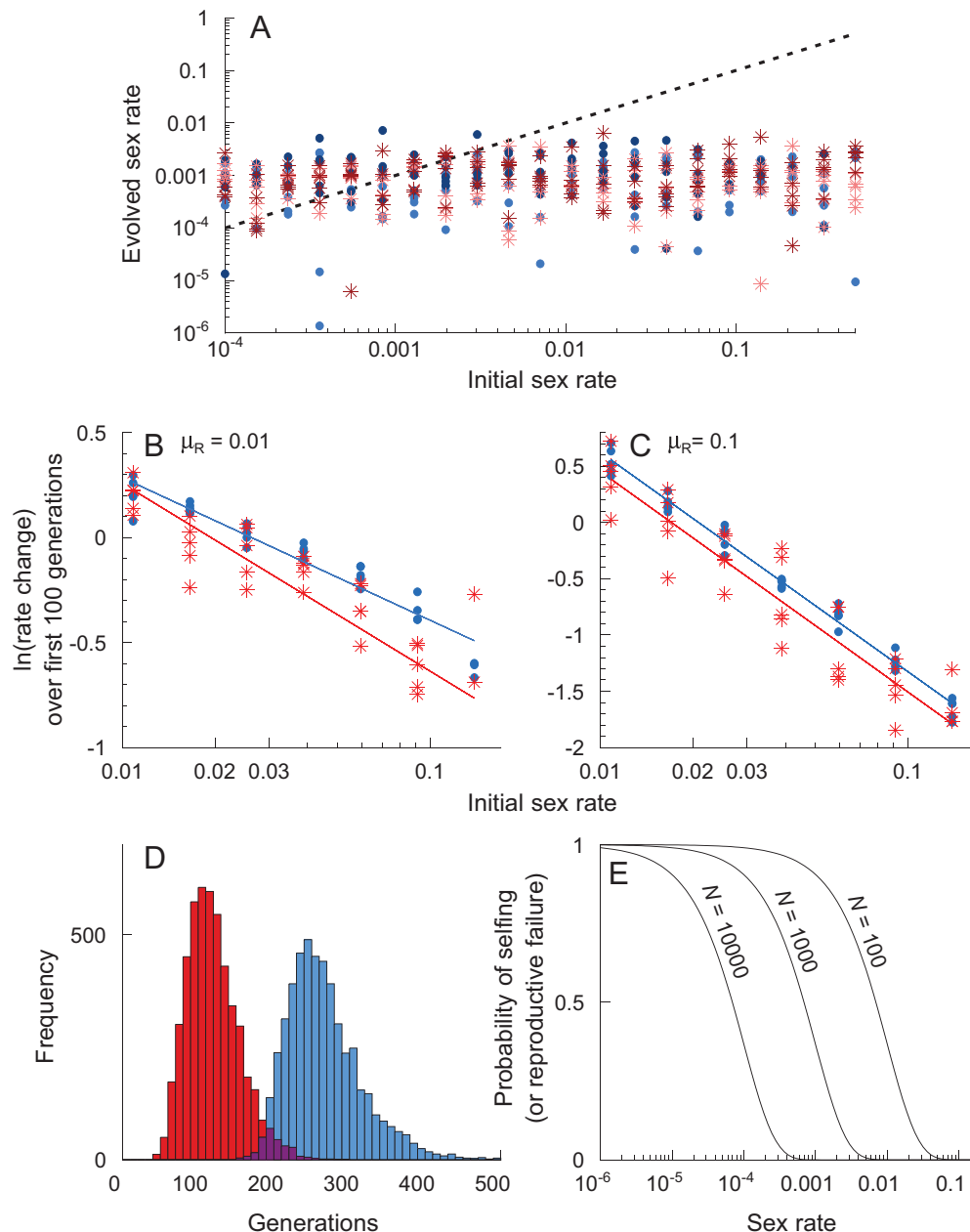
Populations that use a high rate of sex are clearly at risk to turn asexual when there is recurrent mutation to asexuality (fig. 1), but whether resistance to asexuality ceases to be effective above simulations that initiated sex every 1/100 generations, above 1/10, or not at all depends on how rapidly the sex rate can evolve (fig. 1A, 1D: not at all; fig. 1B, 1E: relatively fast; fig. 1C, 1F: fast). The persistence of facultative sex was improved if sex occurred in synchrony. This effect appears very mild if sex rates were not permitted to evolve (compare fig. 1A with fig. 1D), but a logistic regression analysis of the entire data in figure 1 indicates that synchrony and evolution of the sex rate both significantly reduce the parameter area where asexuality can fix (synchrony and evolution both coded dichotomously as yes/no,  $\chi^2 = 193.3$ ,  $df = 2$ ,  $P < .001$ ). All facultative sexuality cases that persisted did so by shifting from the initial



**Figure 1:** Outcomes of simulation runs that ended with either a fitness peak being reached (recorded as 0) or asexual fixation (recorded as 1), with each parameter combination replicated five times. Circle size corresponds to the number of replicates yielding the same outcome, and the red curves, invisible in F, give a fitted probability of fixation based on a logistic regression. *Top row*, asynchronous sex; *bottom row*, synchronous sex; *left*, no sex rate evolution; *middle to right*, increasing mutation rate on sex rates. Other parameters are as follows:  $N = 10,000$ ,  $\mu_A = \mu_B = 10^{-5}$ , and  $c = 0.5$  (i.e., twofold cost of sex).

sex rate (shown by the diagonal in fig. 2A) toward a range of values clearly below 0.01 and centered around 0.001; based on figure 1, rare sex like this keeps asexual invasions ineffective.

Since synchronous and asynchronous sex both evolved similar sex rates (fig. 2A), it is interesting to ask why synchronous sex outperforms asynchronous sex with respect to stability against asexual invasions. Currently existing



**Figure 2:** A, The sex rate (mean of allelic values of facultatively sexual individuals) at the end of a simulation for all evolutionary runs (darker symbols:  $\mu_R = 0.1$ ; lighter symbols:  $\mu_R = 0.01$ ; red stars: synchronous sex; blue circles: asynchronous sex) that did not lead to asexuals fixing (same data as in fig. 1). The diagonal indicates the expectation if the initial sex rate had remained unchanged. B, C, The 100-generation change in the rate of sex, measured as  $\ln(\text{rate at generation 100}) - \ln(\text{rate in the initial generation})$ , depicted for the range where evolving toward a safer rate (see fig. 1) is critical. The data across the entire range is nonlinear (shown in fig. S4) and hence is not suited to a linear regression. D, Toy example of fixation time of a genotype that expresses a maladaptive trait less often (red: synchrony; blue: asynchrony); see main text for details. E, The probability  $(1 - p)^{N-1}$  of a sexual individual, when sex is asynchronously facultative (probability  $p$  for each individual), failing to find a mate (another phenotypically sexual individual) in the same generation.

literature on the genetic consequences of facultative sex is based on asynchrony. This modeling choice tends not to be explicitly justified (Constable and Kokko 2018; Hartfield et al. 2018) and is probably done for the relative ease of finding analytical results for a continual low rate of sex. Based on the meagre differences between figure 1A and figure 1D (both are nonevolving sex rate cases), approximating synchronous rare events with continual low rate of sexual reproduction might indeed often work well. For example, in all the data of figure 1, snapshots every 100 generations show no systematic difference between synchrony and asynchrony with respect to how mean linkage disequilibrium develops over time (fig. S1 shows a comparison for the first 1,500 generations; figs. S1–S4 are available online). Synchrony also does not yield better resistance against asexuality in no-benefit control runs (fig. S2) if sex rates are not evolving, where instead the main determinant of time to asexual invasion (measured as the cumulative number of mutations to asexuality required) is simply the rate of sex: if this rate is very low, the demographic cost is paid rarely, and asexuality takes longer to spread since the dynamics are mostly governed by drift. If sex rates can evolve, this helps sex to resist asexual invasions in the no-benefit scenario but only if sex occurs in synchrony (fig. S2). The protection offered by synchrony, therefore, still needs to be explained. There are at least two possibilities, one occurring at high sex rates, the other gaining importance at low rates.

At high sex rates, the demographic cost of sex is paid frequently, creating selection toward lower rates (fig. 2A), and here synchrony achieves a more rapid response to selection (clearest in fig. 2B where rate mutations occur at a lower rate than in fig. 2C; the difference between the two regression lines is significant,  $P < .001$  in both cases, but only in fig. 2B the slopes differ with  $P < .001$  for the interaction between initial sex rate and synchrony). A similar outcome is found in control runs that strip sex of all its genetic benefits (fig. S2); rapid evolution toward low sex rates can make asexuality an inefficient invader (for a finite time at least, exceeding  $10^4$  accumulated mutations to asexuality in fig. S2).

To understand why synchrony can facilitate the disappearance of maladaptively high sex rates and that this can be purely a consequence of the temporal pattern of when the costs of sex are paid, it is instructive to consider insights from bet-hedging theory (Starrfelt and Kokko 2012). Bet-hedging theory shows that there are situations where arithmetic mean fitness fails as a predictor of long-term evolution. If fitness varies across generations, then generations in which a strategy does poorly (across all individuals adopting this strategy) have a disproportionately strong impact on the long-term prospects; at the extreme, should in a particular generation all individuals fail, the long-term

prospects are zero even if success in other conditions is excellent. Populations with synchronous behavior therefore cannot be analyzed by averaging mean fitness across all conditions, while this approach remains valid for evaluating asynchronous cases. In short, the correct fitness measure (see Starrfelt and Kokko 2012 for caveats) for synchrony is geometric mean fitness, while arithmetic mean fitness can be used for asynchronous cases.

This difference also has consequences for how rapidly populations will adapt. Costs of sex are not constrained to be twofold but can vary due to a large number of ecological causes and within-species idiosyncrasies (Lehtonen et al. 2012; Meirmans et al. 2012). Should its cost have increased (e.g., if a newly invaded predator makes mate searching costlier than before or sex comes with an increased risk of maladaptive hybridization due to the spread of a heterospecific population), it appears that costly sex can respond to selection faster when it is performed synchronously. To understand why, it is useful to simplify away all other interactions (beneficial alleles) and focus on a situation where individuals of a population express a trait either every tenth or every twentieth generation (if the trait is sex, its maladaptive nature here means that the individuals pay the cost of sex). Whenever expressed, the fitness is halved compared to the nonexpression of this trait (this example thus uses a twofold cost, but it generalizes). There are two competing genotypes, one expressing the trait every tenth generation and the other every twentieth generation.

The evolutionary prediction is clear: the genotype with the rarer expression of a maladaptive trait will win. However, the disappearance of the lineage employing a 1/10 rate is faster under the synchrony assumptions that I introduced above than under asynchrony. The geometric fitness values are  $W_{1/20} = 0.9659$  and  $W_{1/10} = 0.9330$ , assuming fitness is scaled to 1 when not expressing the maladaptive trait. Under asynchrony, arithmetic mean fitness remains relevant: expected fitness is  $W_{1/20} = 0.975$  and  $W_{1/10} = 0.95$  in every generation. Although the differences in the degree to which the 1/10 genotype is disadvantaged appear slight between the scenarios ( $W_{1/10}$  is 3.4% lower than  $W_{1/20}$  for the geometric mean but only 2.6% lower when using the arithmetic mean), it is sufficient to yield a marked difference in the number of generations it takes for a finite population to adopt the lower rate (fig. 2D shows time to fixation distributions for  $N = 10,000$ ). Although bet hedging is typically discussed with respect to a bet hedger's chances to spread and fix (Gillespie 1973), in this toy example it helps explain why asynchrony, when interpreted as a form of bet hedging, makes the decline of the 1/10 slower. It uncouples the fates (fitness) of individuals within a generation (see also Schreiber 2015) and thus diminishes fitness differences that act against the 1/10 genotype.



Turning back to our sexual context, this help experienced by high sex rates under asynchrony means that the population is vulnerable to invasion by asexuals for longer, with asynchrony slowing down the response to selection.

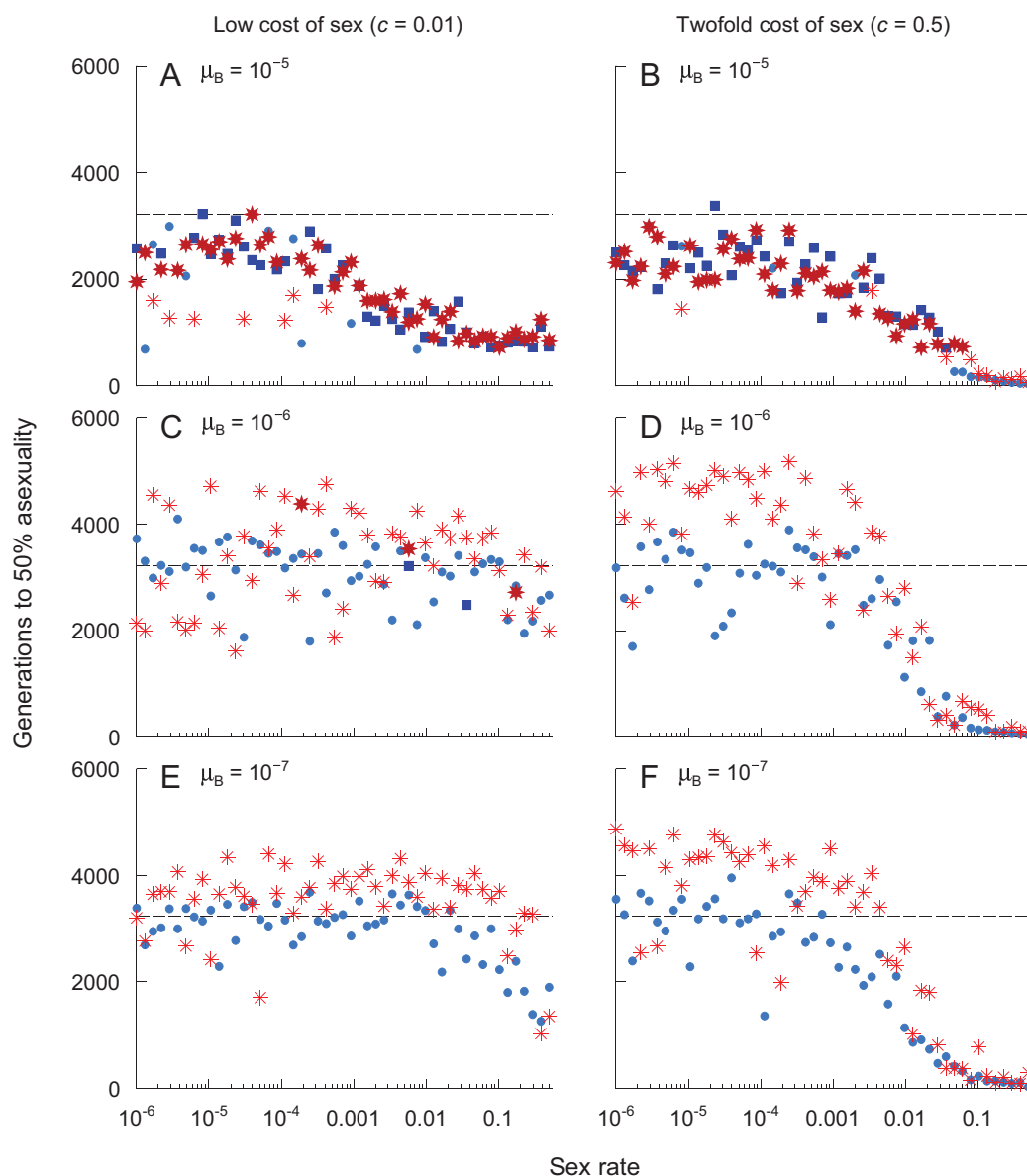
At low sex rates, asynchrony has another, rather obvious but surprisingly little discussed consequence: an individual may find it difficult to find a mate (fig. 2E). The consequences of this depend on model assumptions, and typically, models of facultative sex do not discuss this at all. In the results presented here, selfing was always possible, and while this allows segregation to continue (with certain potential benefits of sex remaining valid; Otto 2003), alternative model assumptions could make low asynchronous sex rates more strongly selected against, if a failure to find a mate leads to reproductive failure. In a simplistic mathematical setting (binomial probabilities underlying fig. 2E), the mate-finding problem remains significant up to sex rates approximately equal the inverse of the population size. Note, however, that population size, in this context, has to be interpreted in the light of mate-searching abilities of the species in question. My models (like many others) use an optimistic assumption that any two simultaneous sexuals are capable of finding each other. Real-life search can be very limited; for example, strains of the facultative sexual pathogen *Podosphaera plantaginis* must coinfect the same plant leaf for outcrossing to occur (Laine et al. 2019). Restricted spatial search is particularly likely to create mate limitation in species that do not perform mating-type switching. The spatial spread of a single mating type under several generations of asexual reproduction can then lead to a spatial structure where neighbors are unable to mate with each other, and this can have major impacts on facultative sex (theory: Constable and Kokko 2018; data: Bell 2005; Nieuwenhuis et al. 2018).

Repeating figure 1 for lower costs  $c$  or lower rates of adaptive evolution  $\mu_B$  yields a similar finding (synchronous sex outperforms asynchronous sex), but comparing the width of parameter regions where asexuality fixes or not yields little insight into the relative stability of facultative sex in any parameter region outside the border of these two dichotomous cases. I therefore next tested for the ability of a fixed (positive) sex rate to resist asexuality when the mutation rate to asexuality continually increases over time, beginning with  $\mu_A = 10^{-5}$  in the first generation and increasing the mutation rate by multiplying with 1.001152 in every generation, this value being chosen to yield  $\mu_A = 1$  in generation 10,000. No facultative sex scenario can persist beyond that, but some succumb much earlier than others, giving a relative stability measure. In sex-neutral control runs, where facultative sex is de facto expressed as asexuality (i.e., sex never expressed) but sex rate alleles can mutate to zero according to the above temporal pattern, individuals with at least one 0 sex allele reach 50%

within 3,220... 3,230 generations (mean 3,226), regardless of  $\mu_B$  (fig. S3).

Turning back to populations where sex is expressed, their relative stability against ever-increasing asexuality pressure can be compared by the time it takes this 50% threshold to be reached. Here I also follow a computational variant of Kreyling et al.'s (2018) argument that potentially nonlinear responses are more usefully studied using a fine-scaled mesh of alternative parameter values and representing each outcome with relatively little (or no) replication than to focus on few extensively replicated locations in the potential parameter space. This comparison yields several clear patterns. High rates of adaptive evolution allow the populations to typically reach the end of the simulation because the fitness peak was reached (by at least one individual) rather than asexuals taking over (fig. 3A, 3B), with the exception of very high rates of sex combined with the high cost of sex (right end of fig. 3B; asexuality wins rapidly here, replicating the no-evolution scenarios of fig. 1). At lower (and perhaps more realistic) rates of adaptive evolution (fig. 3C–3F), the first impression is that asynchronous and synchronous sex offer roughly similar (and intuitively plausible) lessons: high stability against asexuality requires low sex rates if costs of sex are high, while low costs of sex permit facultative sex to be stable across a larger range of sex rates. However, these insights need to be checked against the neutral expectations, and here it is clear that asynchronous sex fails to systematically persist for longer than the neutral scenario would predict (fig. 3).

The success of synchronous sex, on the other hand, is clearly of a stochastic nature: asexuality sometimes outcompetes synchronous sex with ease (i.e., early). This is not surprising at very small sex rates, as synchronous facultative sexuals may phenotypically resemble asexuals for a large number of generations, and sex, when it occurs, can also lead to unfortunate combinations of alleles. In bet-hedging terminology, synchrony is a risk-prone strategy, while asynchrony is risk averse (or risk spreader). As a whole, however, pairwise comparisons where one synchronous and one asynchronous case is investigated for each parameter combination reveal that synchrony significantly prolongs the time until asexuals reach 50% (binomial test  $P = .02, 3.4 \times 10^{-7}, 9.1 \times 10^{-9}$ , and  $1.7 \times 10^{-6}$  for “red above blue” for fig. 3C–3F, respectively, in the case in fig. 3C ignoring the five runs where the simulation ended because a fitness peak was reached). The key difference is that asynchronous rare sex typically leads to a failure to outcross (fig. 2E). In the model, lack of mates led to selfing. Even though this still permits segregation to occur (which can impact selection for sex; Otto 2003), the lack of outcrossing opportunities clearly makes asynchronous sex more vulnerable to asexual invasion (fig. 3).



**Figure 3:** Relative measures of stability of a facultatively sexual population against asexuality when the mutation rate to asexuality  $\mu_A$  increases over time, making it impossible for facultative sex to persist beyond 10,000 generations. Persistence above 3,326 generations (horizontal lines) indicates stability beyond a neutral expectation. Red stars: synchronous sex; blue circles: asynchronous sex; dark red filled stars and dark blue squares, respectively, indicate that the run was finished by reaching the predefined fitness peak. Cost of sex and  $\mu_B$  are as indicated in the panels. Other parameters are as follows:  $N = 10,000$ ,  $\mu_R = 0$  (no evolution of sex rate), and  $\mu_A$  increasing over time as indicated in the main text.

### Discussion

To follow the gist of the symposium, I will discuss both the scientific lessons from the exercise above and end with some general hopes for the future.

First, my model joins many others in not resolving the entire issue of why we are not all facultatively sexual, in the following sense: while rare sex appears relatively easy

to maintain, obligate sex did not evolve in my model, and it is generally difficult to find obligateness in models of sex whenever facultativeness is an option. This points out that the entire question might be usefully rephrased: rather than asking what keeps facultative sex rare, an unresolved question is why obligate sex can at least sometimes replace it, often taking over entire lineages (so that large multicellular organisms such as ourselves perceive

it to be the norm; Kokko 2017). Eukaryotic life in general utilizes facultative sex much more commonly than a focus on large, multicellular animals or plants would suggest (Hastings 1992; Dacks and Roger 1999). When viewed across a broad-enough taxonomic lens, sex also does not necessarily associate with the production of males. Sexual conflict, where males benefit from mating while females might not, can complicate the maintenance of facultative sex (Gerber and Kokko 2016; Burke and Bonduriansky 2017), but this argument only applies to species with males (anisogamy). Science has made some progress toward understanding why anisogamy associates with being large and multicellular (Lehtonen and Parker 2019); why this should also often associate with obligate sex is an obvious follow-up question.

Second, it may be useful to think of the demographic and genetic consequences of synchronous facultative sex. Real sex often occurs in bursts (sexual generations followed by many largely asexual ones), and this has several consequences. One consequence is that the evolution of sex could usefully be better linked with bet-hedging theory, a mathematical framework investigating the success of competing genotypes that differ in mean fitness as well as variance. While sex does not get straightforwardly explained as soon as this is done (examples by Li et al. 2017), bet-hedging considerations apply if sex has an impact on both the mean and the variance of offspring production. Synchrony changes the temporal dynamics of a population such that geometric mean fitness becomes relevant; that is, low demographic performance in any one generation has a significant detrimental effect on long-term prospects. In the current model, the effect was, perhaps counterintuitively, ultimately a stability-enhancing one for facultative sex, as asexuals invaded risk-prone (synchronous) populations less easily than risk-averse (asynchronous) ones. Because asynchronous sexuals may also more often have to resort to selfing, if selfing is an option, the balance of these effects could be usefully studied in future studies.

Another consequence of an explicit contrast of synchrony and asynchrony is to encourage explicit thinking about mate availability in model assumptions. Many existing models of sex simply sidestep this issue, in the sense of assuming random mating or (in anisogamous models) that better males will be chosen as mates more often (e.g., Agrawal 2001; Kleiman and Hadany 2015); the consequences of no mates being found at all are usually not specified. The model presented in this article dealt with mate shortages by assuming that selfing was always an option, but diversity in nature offers multiple alternative assumption sets that could be usefully investigated in the future (e.g., many apomictic plants still produce pollen and can thus act as sires even if their female function is asexual).

It is instructive to reflect why mate availability is rarely considered. Analytical simplicity is one reason, potentially wholly justified if the focus is on another question. Another reason, harder to verify but probably real, is the mental images employed by any modeler thinking about what to include in a model and what to leave aside. One researcher might be thinking of a large population of eukaryotic microbes going for sex simultaneously, in which case synchrony might not be assumed in a model yet its occurrence in real life creates an impression that mate availability is not limiting whenever sex actually happens. Another researcher might mostly think about large multicellular organisms, and the corresponding mental image now features a female (or the female function of a hermaphrodite) that, when opting for sex, will not typically encounter a shortage of males. Neither mental image is conducive for remembering that access to partners can easily become lopsided based on purely stochastic processes, particularly so if much of reproduction is asexual (Bell 2005; Constable and Kokko 2018; Nieuwenhuis et al. 2018). Specific adaptations exist that may alleviate the problem (e.g., mating-type switching; Nieuwenhuis and Immler 2016); linking these with the evolution of sex rates would appear worthwhile.

Synchrony, in this light, makes sense as it eases the problem of mate finding, but real life offers additional complications related to access to mates. Sex is often not solely triggered by environmental conditions but can also be condition dependent, often such that organisms in a favorable state opt for asexual reproduction. Assuming that condition reflects how well an organism is currently adapted to its surroundings, then condition-dependent sex presents an intriguing dilemma: recombination will occur only among the poorly adapted part of the population; how much is it then expected to help? Hadany and Otto (2007, 2009) have shown that the problem is not insurmountable, as condition-dependent sex can spread despite not having access to the very best genotypes. It would clearly be of interest to combine such work with considerations of synchrony and mate finding (especially since synchrony itself might evolve if organisms switch to sex during times when its costs are unusually low, as suggested for *Daphnia*, where the cost of sex is effectively lowered when high population density makes asexual direct reproduction relatively unprofitable; Gerber et al. 2018).

Spatial considerations are an obvious problem when specifying the mate-finding range, and it offers additional real-life flavors to be included in models. Dispersal (escaping in space) and dormancy (escaping in time) offer alternative ways to condition-dependent sex of dealing with low current fitness prospects, and in many within-species settings, they covary strongly with sex itself (Gerber and Kokko 2018). Exactly why organisms so often use sex—interpretable as an abandon-ship mechanism—together

with these other ways to escape their current situation is largely unexplored; if each mechanism brings about costs, one might a priori expect employing just one of them would suffice. Finally, note that the problem of access to the well-adapted part of the local gene pool might disappear in some formulations of condition-dependent sex: hermaphrodites can conceivably be facultatively sexual with respect to their female function but always willing to mate in the male role. In systems where some potential mates are rejected (for displaying signals of low condition), condition dependence takes yet new forms.

The above is a short list of reasons why the question of facultative sex is far from resolved. It rarely evolves all the way up to obligate sex (though for the ability of sexual selection to select for high rates, see Kleiman and Hadany 2015), but this is only one of the many problems in the field. Life abounds with across-species correlations begging to be explained: my model, by presenting a few examples on the possible effects of synchrony, did not even try to ask why there is more obligate sex in larger, anisogamous organisms or extend the stability question to the possible covariation of reproductive mode with survival structures and/or dispersal (here relevant literature will also need to include reproductive assurance provided by asexuality; Tilquin and Kokko 2016). In short, natural history (Futuyma 1998) will hopefully continue to inspire and make theoreticians exist in a delightful tug-of-war between analytical tractability and real-life complications.

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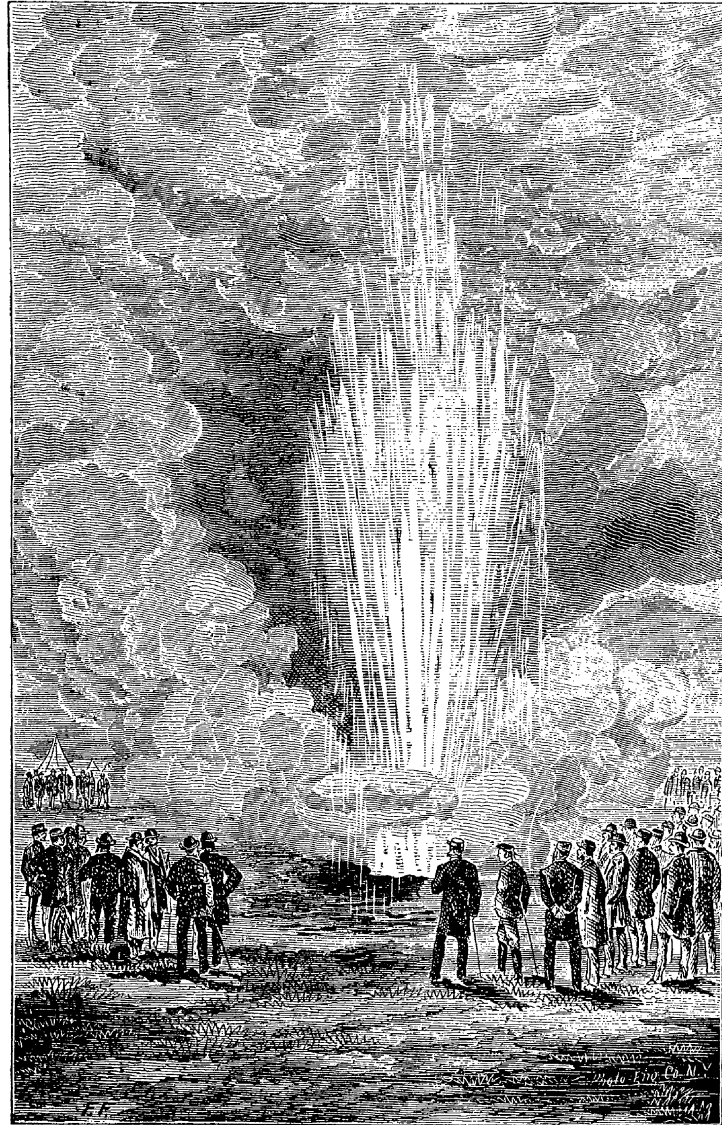
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“Our readers will examine with much interest the chapter on the Physical Characters of Iceland, in which the author adopts the view that Iceland was uplifted towards the end of the glacial epoch, and that this explains the traces of a milder climate in Greenland before the advent of man.” Figured: “Eruption of Strokr, Aug. 5, 1874.” From the review of Kneeland’s *American in Iceland* (*The American Naturalist*, 1876, 10:296–297).